A CASE STUDY OF THE SALTWATER CROCODILE *CROCODYLUS POROSUS* IN MUTHURAJAWELA MARSH, SRI LANKA: CONSIDERATIONS FOR CONSERVATION[1]

DENI POREJ[2]

[1]Accepted May, 2003
[2]The Nature Conservancy, 6375 Riverside Drive, Dublin, OH 43017, USA.
Email: dporej@tnc.org

Muthurajawela Marsh - Negombo Lagoon is a 6,300 ha complex consisting of a brackish marsh and a shallow lagoon, located just 20 km north of Colombo, the capital of Sri Lanka. I located and studied a small, remnant population of saltwater crocodile (*Crocodylus porosus*) in this complex. The total number of adults is estimated to be 15 individuals (estimated up to 33 individuals at a 95% C.I.), and this population is still reproducing. Human activities are reducing breeding success in the otherwise suitable habitats (reed islands, mangrove forest), directly (hunting and fishing), and indirectly (habitat modification). Killing of nest-guarding female crocodiles and capture of juvenile crocodiles in "brush piles" are the two most detrimental hunting practices. Better understanding of these small-scale processes may help explain the gradual decline of saltwater crocodiles on a large scale in Sri Lanka, and offer guidance for developing effective conservation programmes.

Key words: Conservation, crocodile, *Crocodylus porosus*, Sri Lanka, wetland

INTRODUCTION

Two species of crocodile, the mugger or marsh crocodile (*Crocodylus palustris*) and the saltwater crocodile (*Crocodylus porosus*), inhabit Sri Lanka. Historically, information on the status of these species in Sri Lanka has been scanty (Deraniyagala 1953, Whitaker and Whitaker 1979), but for some recent data (Porej 1997a, Santiapillai *et al.* 2000, Santiapillai and de Silva 2001). Both crocodile species are currently listed in Appendix I of CITES for Sri Lanka (Convention of International Trade in Endangered Species of Wild Fauna and Flora). Santiapillai and de Silva (2001) estimate the total number of saltwater crocodiles in Sri Lanka to be perhaps no more than 300, and suggest that this species be considered "critically endangered" within Sri Lanka.

Saltwater crocodiles are the most widely distributed of the crocodilians, ranging from southern India and Sri Lanka, throughout southeast Asia and the Indo-Malay Archipelago, to the Philippines, New Guinea and northern Australia (Ross 1998). Their status is highly variable, from being virtually extinct in some countries (Singapore, Thailand) to abundant in others (e.g. Australia). Although there are numerous national parks in Sri Lanka, and crocodiles are protected by the Fauna and Flora Protection Ordinance of 1938, there are no conservation or management programmes in place. Saltwater crocodiles have been extirpated or severely reduced in several areas around the island, and persist mainly in isolated patches of suitable habitat, and remote areas where human activity is still low (Whitaker and Whitaker 1989, Porej 1997a, b). Fishing, hunting and habitat modification were identified as leading causes for the decline of saltwater crocodiles in Sri Lanka (Uragoda 1994, Santiapillai and de Silva 2001). Illegal crocodile hunting occurs in most of the 26 wetlands surveyed by Porej in 1997 (Porej 1997b, see also Santiapillai and de Silva 2001). In a recent synthesis of crocodile data from Sri Lanka, Santiapillai and de Silva (2001) documented crocodile decline and noted that the amount and distribution of protected areas in the western, southwestern, and southern areas of the island remain inadequate. Obtaining quantitative data on saltwater crocodile distribution and abundance in Sri Lanka has been identified as a high priority by the IUCN Crocodile Specialist Group (Ross 1998).

The saltwater crocodile population of the Muthurajawela Marsh-Negombo Lagoon complex (MNLC) inhabits an area in which some prime habitat remains only because the area's physical characteristics (constant flooding, poor soils, difficult access) render it unsuitable for agriculture and large-scale timber exploitation. Like many other river estuaries on the western and southern Sri Lankan coast, where saltwater crocodiles still persist (Porej 1997a, Santiapillai *et al.* 2000), this area is almost completely isolated by surrounding human activities (Samarakoon and van Zon 1991). It is likely that massive residential and industrial developments, which tend to concentrate in these areas, disrupt normal migratory patterns along the upstream waterways (Ross 1998). In addition, crocodile populations in areas such as the MNLC face increased hunting pressure as the surrounding human population increases, and road developments provide access to previously inaccessible crocodile foraging and breeding grounds.

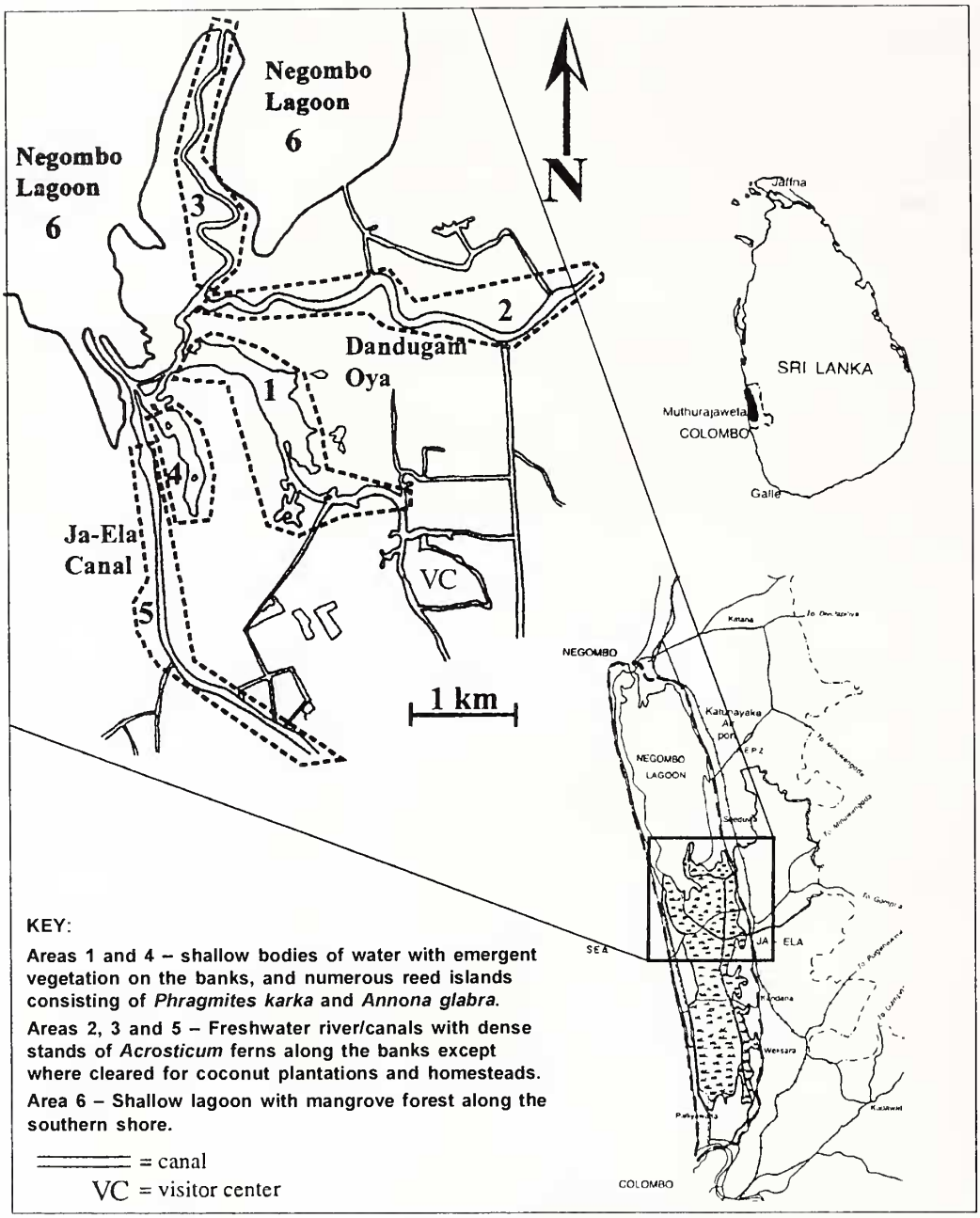

Fig. 1: Map of Muthurajawela Marsh- Negombo Lagoon complex, Sri Lanka, showing the location of six survey areas

This case study investigates the effects of human activities on crocodile distribution, breeding activities and population numbers on a local scale. Questions of interest are: How much overlap exists between fishing areas and suitable crocodile breeding habitat in estuarine regions such as MNLC? Do relatively low-impact, small scale hunting and fishing practices affect local crocodile populations? If so, what are the most detrimental fishing/hunting practices, and how can they be modified to allow the coexistence of man and crocodile? Better understanding of these local processes can help explain the gradual disappearance of saltwater crocodiles on a large scale from Sri Lanka, and help devise more effective conservation plans.

STUDY SITE

The Muthurajawela Marsh-Negombo Lagoon complex (MNLC) is located *c.* 20 km north of Colombo, capital of Sri Lanka. It consists of the Muthurajawela marsh, a large area of brackish marshes (3,100 ha) on the southern end, and the shallow (avg. depth 0.65 m), estuarine Negombo lagoon (3,200 ha) to the northwest (Fig. 1). The lagoon opens into the sea by way of a single opening at the northern end.

The Muthurajawela marsh consists of previously cultivated rice paddy fields, a network of canals, scattered ponds and cultivated fields. Most of the Muthurajawela marsh is flooded during the periods of heavy rain, and the poorly drained peat substrate is saturated almost the whole year. Large areas of natural vegetation still exist, particularly in the northern segment of the marsh. The southern portion of the marsh is dominated by a combination of sedges and cattails. Also common are patches of ferns (*Acrostichum aureum*) and an invasive, exotic shrub *Annona glabra*. Mangroves still fringe some segments of the lagoon shoreline.

The MNLC harbours immense bird diversity (146 resident and 35 migrating species) and is productive enough to support over 3000 fishermen (Samarakoon and van Zon 1991). In addition to saltwater crocodiles, it provides habitat for an assemblage of wetland-dependent reptiles and amphibians. These include two species of monitor lizards, two endangered terrapins, and the extremely rare Gerard's water snake *Gerarda prevostiana* (Porej 2001).

The study site was divided into 6 study areas differing in physical characteristics (Fig. 1.) and ranging from river and canal (areas 2, 3 and 5) to shallow, slow-flowing or stagnant open water bodies (areas 1, 4 and 6). These areas also differ in the amount of housing and the intensity of fishing activities. Most houses are located along the banks of the Dandugam. Oya River and the Ja-Ela canal. Of 173 houses located within the boundaries of the study site, 135 (78%, 22.5 houses/km riverbank) are located along the canal in area 5; 17 houses are located in area 2 (9.8%, 4.7 houses/km riverbank); and the rest are squatters' houses scattered throughout the more remote areas (Samarakoon and van Zon 1991, Benthem and van Zon 1994).

Fishing methods include push nets, seines, cast nets and brush piles, (Samarakoon and van Zon 1991). Brush piles and harvesting of females guarding a nest are two methods by which crocodiles are captured in the MNLC. Brush piles are fish-aggregating devices, constructed by forming a 5-6 m diameter circle of upright sticks in shallow water, and filling it with small branches and leaves. Decomposing material attracts many small fish and shrimp to these sites, which in turn attract large fish favoured by fishermen. After a period of 30-45 days brush piles are surrounded by fishing net, the branches removed, and the fish captured by hand or hand-held nets. Quite often, juvenile crocodiles take refuge in these 'havens' and become a welcome addition to the fisherman's diet. Adult crocodiles taken are mostly females killed while guarding a nest. When a nest is discovered, the fishermen will return to the site until they locate and kill the female. If the eggs are recently laid, they are collected for consumption, and if not, the nest is usually set on fire.

MATERIAL AND METHODS

Study areas were surveyed eight times from May 7 to August 18, 1997. Surveys were carried out at night from a boat moving at constant speed (*c.* 10 km/h), using a 1 million candlepower searchlight (for a detailed description of night-time survey techniques and techniques for the capture and restraint of crocodilians see Bayliss 1987 and Crocodile Specialist Group 1994). Every 20 minutes of the survey, water and air temperature, cloud cover, tide level and wind speed were recorded, along with a short description of the physical features (bank characteristics, vegetation, wind, light and tide level). These data are available upon request. Surveys were carried out within 3 hours of low tide, but due to abundant vegetation, low tide usually exposed only 20-30 cm of bank.

An observed crocodile was approached until it submerged or was captured. Observation distance (distance from the observer to the crocodile) was recorded, and detected individuals were entered into one of four size categories (adapted from Crocodile Specialist Group 1994) of estimated total lengths shown in Table 2. In Sri Lanka, saltwater crocodiles reach sexual maturity by the time they are 1.7 to 2.7 m in total length (see Deraniyagala 1953, Santiapillai and de Silva 2001). Animals less than 50 cm long were classified as juveniles, and animals in the range of 50-200 cm were considered sub-adults. Animals that were not approached close enough to record exact size were recorded as "Eyes only" (E.O). Adult crocodiles are wary of humans, and individuals in this group were almost always large, exceeding 2 m in length, which submerged within moments of being spotted. Records of "Eyes only" were therefore added to the adult count (Webb and Messel 1979, Sah and Stuebing 1996). Captured individuals were measured (total length, SVL, weight) and marked by clipping a combination of dorsal scutes, then released. No individuals were recaptured.

The calibration method of Messel (1979), and Messel and Vorlichek (1989) was used to estimate adult population in the MNLC. Because of the constant fresh water input, this complex would be considered a Type I waterway in their classification, and appropriate calibration formulas were used (Webb and Messel 1978). Differences in observation distances among study sites were examined using one-way ANOVA after testing for homogeneity of variance using Bartlett's test. A Spearman rank order correlation test was performed on the ranked scores for the adult and non-adult (juvenile and sub-adult densities combined) densities observed within an area. Means are followed by ±1 SD, unless noted otherwise.

Active (with eggs) and inactive nests were located by interviewing fishermen, using boats or by walking along shores, riverbanks, and canals with permanent water, and looking for a smooth slope with slide marks into the water or well-worn tracks. Previous studies have reported that female *C. porosus* may build multiple nests (Webb *et al.* 1983), and therefore the extent to which the located nests reflect the total number of nests in not known.

The number of brush piles was recorded during each survey, and an average was calculated for each study area. As a part of a different study (Porej 2001) most study areas of the marsh were visited every day, and during these visits every instance where a fish net was placed across the entire width of the northern entrance to areas 1 or 4 was recorded.

RESULTS

Crocodile survey

The mean number of crocodile sightings was 11 ±3.8 per survey (Table 1). Juveniles and sub-adults made up 78% of the total sightings (Table 2). Mean observed densities were 0.21 ±0.1 individuals/km for adult crocodiles and 0.73 ±0.6 individuals/km for juveniles and sub-adults combined. The highest density of adults was recorded in areas 2, 3 and 4, and non-adult density was highest in areas 2 and 4.

The average distance from which a crocodile was first observed was 26 ±11 m. There is no significant difference in average observation distance among study areas ($F_{5, 81}$ 0.507, p = 0.23, one-way ANOVA). There was a statistically significant correlation between adult and non-adult densities observed within each area (r = 0.89, p = 0.015, df = 4, Spearman rank-correlation test). A notable outlier is area 3, which had a lower density of non-adults than would be expected from the observed adult density (adult density ranked 1st and non-adult density ranked 3rd).

Table 1: Crocodile sightings during 8 surveys from May to August 1997 in MNLC

Survey date	Survey Area 1	2	3	4	5	6	Total adults	Total (non adults)
May 7-8	1	3	2(1)	2	2	0	1	9
May 19	1	11	1	2(2)	-	-	2	13
May 26-17	2(2)	12(4)	-	0	1	0	6	9
June 5	1	-	3(2)	2	2(2)	2	4	6
June 19-20	1	-	2	0	-	3(2)	2	4
July 3-4	2	6(1)	2	1	1	1	1	12
August 2-3	0	4	-	1	2	-	0	7
August 18	1	5(1)	4(2)	2	-	0	3	9
Density (adults)	0.14	0.33	0.33	0.28	0.07	0.11	0.21	
Density (non-adults)	0.39	1.94	0.60	1.00	0.20	0.22		0.73

Number of adults and "Eyes Only" individuals are given in parenthesis.
Density is expressed as number of individuals/km of shoreline surveyed.
Waterways not surveyed are marked "-".

The total number of adult crocodiles inhabiting the marsh is estimated at 15 (the 95% C.I. estimates the number of adults to be up to 33). During the additional three surveys of Dandugam Oya upstream from Muthurajawela, only two adult crocodiles were observed over 32 km of river surveyed.

A total of 11 nests (9 active) were recorded (Table 2), only two of which were successful.

Fishing

The average density of brush piles was 5.2/km in area 1, 2.3/km in area 4, and less than 0.8/km in remaining areas. Fishing nets were cast across the entire canal width at the entrance to area 4 for 17 days (out of 107 days), and for 65 days at the entrance to area 1.

DISCUSSION

Compared to the results from other standardized saltwater crocodile surveys for these types of systems (e.g. Bayliss and Messel 1988), crocodile densities in the MNLC are at the lower end of the range. In spite of all the past and present habitat modifications, the MNLC still possesses fairly large areas of physically suitable crocodile breeding habitat, and this population still manages to reproduce successfully, despite the low numbers.

Webb *et al.* (1983) identified seven common aspects of *C. porosus* nest site vegetation, and according to these criteria, study areas 1 and 4 (dense vegetation, protected islets, slow water flow), and areas 2 and 5 (dry riverbanks) are expected to be prime breeding areas. While similar in habitat composition, these areas differ in their levels of human activity, and offer some insights into the possible effects of fishing and housing on the crocodile distribution within MNLC.

In areas 1 and 4, the understorey is sufficiently dense and at least 1.5 m high. *Phragmites karka* is abundant, the roots of *Annona glabra* can provide nest support, and there is plenty of direct sunlight. While these two areas consist of very similar habitat, area 1 had 2.3 times the density of brush piles. During this study, the entrance to area 1 was blocked by fishing nets almost 4 times more often than the entrance to area 4. Lower densities of both adults and juvenile crocodiles

in area 1 can therefore likely be attributed to the more intensive fishing in this area.

Areas 2 and 5 consist of comparable habitat as well, but here the main human activities are not hunting or fishing, but spread of squatters' settlements and coconut plantations that tend to occupy all available dry ground. Permanent dry ground close to roads and main waterways is the most valuable asset in the whole region, and quickly attracts more settlers to both these areas. Currently, housing density is 4.8 times higher in area 5, and this difference is associated with a six and ten-fold decrease in observed adult and juvenile densities respectively. Area 2 is becoming increasingly populated, and cessation of crocodile breeding is likely, as has already happened in area 5, where the last nesting attempt was in 1992.

Area 3 is a section of Dandugam Oya River closest to the lagoon, and under significant tidal influence, with pronounced fluctuation in water level. Flooding can have a devastating effect on *C. porosus* eggs, killing up to 80% of all embryos in some regions. This area had a lower density of non-adults than would be expected from the observed density of adults, and 3 out of 4 nests were flooded during the course of the study. Therefore, although this area is remote and fishing is not intensive, it should be considered sub-optimal breeding habitat.

Unlike the mangrove forests elsewhere around the marsh complex, area 6 has not been destroyed, as it has no permanent and convenient road access (see Fig 1).

Flooding and lack of suitable nest material, such as grasses or herbs (Webb *et al.* 1977) can explain the scarcity of crocodile nests in the mangrove forest. In addition, small outrigger canoes used by fishermen are ideal for penetrating deep into the forest interior, allowing easy access to even the most remote sections. Consequently, crocodile nesting sites in this area are all well known and have been exploited for years. Fishermen destroyed both active nests in this area before the eggs hatched.

Conservation considerations

Although a conservation management plan for the MNLC has been proposed (Benthem and van Zon 1994), it does not include any special provisions for the remnant crocodile population. Incorporating a crocodile component into the general conservation plan for the area would strengthen the plan and assure that this genuine opportunity is not missed. Three key components would be: a) preservation and enhancement of critical breeding habitat, b) education, and c) close cooperation with local people through a comprehensive management plan (possibly including sustainable use) to ensure continued survival of this population.

Habitat preservation and enhancement

The data from this survey demonstrate a negative association between crocodile density and the intensity of human activities (fishing and housing), and indicate that some of the areas are being overexploited. Reducing juvenile and nest mortality should be the first step in securing the survival of this population. In addition, since female *C. porosus* spend the dry season in regions suitable for nest construction in the wet season, and selection of a freshwater site during the dry season may ultimately determine the location of their nest in the wet season (Webb *et al.* 1983), some presence of adult females in suitable breeding areas needs to be tolerated throughout the year. Both of these goals could be achieved by preventing further spread of squatters' settlements along Dandugam Oya River (western portion of area 2), and by regulating fishing activities in areas 1 and 4 (perhaps initially by prohibiting the practice of placing fishing nets across the entire width of canals, which would allow some free movement of adults in and out of this area at all times).

Education opportunities

The Muthurajawela Visitor Centre was set up in 1996,

Table 2: Observed active nests and crocodile sightings by size class in 6 study areas

	Size class					Nests		
Area	0-50	50-150	150-200	200-250	E.O.	Destroyed	Flooded	Successful
1	6	1	0	1	1	-	-	-
2	22	10	3	2	4	1	-	1
3	5	3	1	2	3	1	3	-
4	7	0	1	0	2	-	-	1
5	3	5	0	1	1	-	-	-
6	2	1	1	0	2	2	-	-
Total	45	20	6	6	13	4	3	2

Sizes are given as total length (cm),
E.O. indicate individuals who were positively identified as crocodiles, but submerged before their size was measured or visually estimated

and thousands of visitors (including 14,000 school children in 1997 alone) come every year for a scenic bird watching boat ride or stroll along the nature trails, guided by trained local residents. MNLC is close to Sri Lanka's capital city Colombo, with numerous hotels on the west shore, and most foreign tourists pass it on their way to and from the Katunayake International Airport. The Visitor Centre currently serves to educate tourists, visiting public and local fishermen alike.

Management considerations

It is ironic and possibly instructive that "in the countries where *C. porosus* is heavily but sustainably used, it is secure, but in the countries where it is completely but ineffectively protected, it may disappear" (Thorbjanarson 1992). Previous studies on crocodiles in Sri Lanka (Wikremasinge and Santiapillai 1999, Santiapillai and de Silva 2001) point out that in the absence of economic incentives at a local level, no amount of legislation will ensure the long-term survival of crocodiles outside the protected areas. Crocodilians, because of their high reproductive rates and valuable skin and meat, have considerable potential for sustainable use and management (Webb and Manolis 1993, Thorbjanarson 1992), and several successful sustainable use programmes have been implemented elsewhere (Bolton 1988, Jenkins 1994). Given its proximity to Colombo and other tourist hotspots, popularity, and the relatively poor agricultural potential of this area, MNLC might be the perfect launching site for the first project of this kind in Sri Lanka.

ACKNOWLEDGEMENTS

I thank Sumeddha Devappriya for being a great friend and an excellent field assistant, and the staff of the Muthurajawela Visitor Centre for assistance during fieldwork. I thank the fishermen of MNLC for trusting me, and for many very informative discussions about hunting and living with crocodiles (after assuring themselves that I was not working for the police). Dr. J.P. Ross of the Crocodile Specialist Group provided expert guidance throughout this project. The Wetland Conservation Project and Dr. Samarakoon provided moral, financial and logistic support. I thank T. Hetherington and B. Coupe (OSU), G. Rodda (USGS), and J.P. Ross (CSG, University of Florida). This work was funded by ENERGOPROJEKT (Belgrade, Yugoslavia) and The Wetland Conservation Project (Sri Lanka). Hvala Poreji!

REFERENCES

Bayliss, P. (1987): Survey methods and monitoring within crocodile management programmes. Pp. 157-175. *In*: Wildlife Management: Crocodiles and Alligators (Eds: Webb, G.J.W., S.C. Manolis and P.J. Whitehead). Suffet Beatty & Sons Ltd. Chipping Norton, Australia.

Bayliss, P. & H. Messel (1988): The population dynamics of the estuarine crocodiles. 1. An assessment of long-term census data. Pp. 102-139. *In*: The Proceedings of the 9th Working meeting of the crocodile specialist group of the Species Survival Commission of the IUCN, Vol. 1. Lae, New Guinea.

Benthem, W. & J.C.J. van Zon (Eds.) (1994): Conservation Management Plan - Muthurajawela Marsh and Negombo Lagoon. Central Environmental Authority / Euroconsult, Colombo, Sri Lanka.

Bolton, M. (1988): The role of crocodile ranching in rural development. Pp. 89-99. *In*: The Proceedings of the 9th Working meeting of the crocodile specialist group of the Species Survival Commission of the IUCN, Vol. 1. Lae, New Guinea.

Crocodile Specialist Group (1994): Guidelines for monitoring crocodilian populations. Pp. 550-585. *In*: Crocodiles: Proceedings of the 2nd Regional (Eastern Asia, Oceania, Australasian) Meeting of the Crocodile Specialist Group. IUCN - The World Conservation Union, Gland, Switzerland.

Deraniyagala, P.E.P. (1953): A coloured atlas of some vertebrates from Ceylon, Vol. 2. Ceylon National Museums Publication, Colombo, Sri Lanka.

Jenkins, R.W.G. (1994): Sustainable use of crocodilians: conservation benefits. Pp. 161-169. *In*: Proceedings of the second regional meeting of the Crocodile Specialist group. World Conservation Union, Gland, Switzerland.

Messel, H. (1979): Monograph 1. Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. Pergamon Press, Sidney, Australia. 39 pp.

Messel, H. & G.C. Vorlichek (1989): Status and conservation of *Crocodylus porosus* in Australia. Pp. 187-199. *In*: Crocodiles: their ecology, management and conservation. IUCN, Gland, Switzerland.

Porej, D. (1997a): Sri Lanka: Crocodile survey and public relations program. *Crocodile Specialist Group Newsletter 16(3)*: 9-10.

Porej, D. (1997b): Status of saltwater crocodiles in wetlands of the southern Sri Lanka. Report to the Sri Lanka Department of Wildlife Conservation and the Wetlands Conservation Project. 14 pp.

Porej, D. (2001): Herpetofauna of the Muthurajawela marsh - Negombo lagoon, with notes on natural history. *Herpetological Natural History 8(1)*: 27-35.

Ross, J.P. (Ed.) (1998): Crocodiles: Status Survey and Conservation Action Plan, 2nd (web) edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland.

Sah, S.A.M. & R.B. Stuebing (1996): Diet, growth and movements of juvenile crocodiles (*Crocodylus porosus*) Schneider in the Kilas River, Sabah, Malaysia. *Journal of tropical ecology 12*: 651-662.

Samarakoon, J. & H. van Zon (Eds.) (1991): Environmental Profile of Muthurajawela and Negombo Lagoon. Greater Colombo Economic Commission, Colombo, Sri Lanka. 230 pp.

Santiapillai, C. & M. de Silva (2001): Status, distribution and conservation of crocodiles in Sri Lanka. *Biological Conservation 97*: 305-318.

Santiapillai, C., M. de Silva, M. Dissanayake, S. Jayaratne & S. Wijeyamohan (2000): An ecological study of crocodiles in the Ruhuna National Park, Sri Lanka. *J. Bombay Nat. Hist. Soc. 97(1)*: 33-41.

Thorbjanarson, J. (1992): Crocodiles: An action plan for their conservation. IUCN. Gland, Switzerland. 136 pp.

URAGODA, C.G. (1994): Wildlife conservation in Sri Lanka. Wildlife and Nature Protection Society, Colombo, Sri Lanka.

WEBB, G.J.W. & H. MESSEL (1978): Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Aust. Wildl. Res. 5*: 263-283.

WEBB, G.J.W. & H. MESSEL (1979): Wariness in *Crocodylus porosus* (Reptilia: Crocodilidae). *Australian Wildlife Research 5*: 263-283.

WEBB, G.J.W., H. MESSEL & W. MAGNUSSON (1997): The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. *Copeia 2*: 238-249.

WEBB, G.J.W., G.C. SACK, R. BUCKWORTH & S.C. MANOLIS (1983): An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Aust. Wildl. Res. 10*: 571-605.

WEBB,G.J.W. & S.C. MANOLIS (1993): Conserving Australia's crocodiles through commercial incentives. Pp. 250-256. *In*: Herpetology in Australia: a diverse discipline. (Eds: Lunney, D. and D. Ayers). Transactions of the Royal Zoological Society of New South Wales, Mosman, Australia.

WHITAKER, R. & Z. WHITAKER (1979): Preliminary crocodile survey-Sri Lanka. *J. Bombay Nat. Hist. Soc. 76(1)*: 66-85.

WHITAKER, R. & Z. WHITAKER (1989): Status and conservation of the Asian crocodilians. Pp. 297-308. *In*: Crocodiles: their ecology, management and conservation. IUCN, Gland, Switzerland. 308 pp.

WICKREMASINGHE, C.S. & C. SANTIAPILLAI (1999): Can wildlife pay for its conservation? *Loris 22(2)*: 18-22.

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